Pacific Island Forests: Successionally Impoverished and Now Threatened to Be Overgrown by Aliens?[1]

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Abstract: Indigenous forests in remote islands are generally impoverished of secondary successional tree species. After canopy disturbances, the same indigenous tree species seem to resume dominance by a process known as "autosuccession" or "direct succession." Primary forest tree species are mostly colonizer species. Mature island forests are difficult to categorize as either pioneer, successional, or climax forests by their canopy species composition. Climax forests, which characterize mature forests in less-isolated areas, are typically of distinctly different canopy species composition than the pioneer forests. In central Canada, for example, pioneer pine forests are replaced in succession by mixed hardwood/softwood forests under exclusion of fire. This process is known as "normal replacement succession" or "obligatory succession." Another well-known ecological concept distinguishes between "primary" and "secondary" forests in the continental tropics. Secondary forests are formed by fast-growing relatively short-lived second-growth species, which quickly assemble after major disturbances. It usually takes a long time for primary tropical rain forest trees to reappear in secondary forests. In contrast, primary island forests rarely include fast-growing indigenous canopy species that form such secondary forests in the continental tropics. Instead, secondary forests in islands are now made up mostly of introduced species. In this paper I attempt to evaluate alien plant invasion in remote islands in view of these concepts of ecological succession.

In most islands, the isolation barrier has been broken by the anthropogenic introduction of alien species. Some of the introduced species have become invasive. In spite of successful control efforts, a new natural nonstoppable dynamic has been unleashed by humans through the introduction of invasive species. Questions arising are, Will alien species behave like second-growth species in the continental tropics or will they replace all native island vegetation? What can we predict about forest succession in islands under the added complexities of global change?

To elucidate these questions, I will first refer to the island biogeography model with regard to vegetation development. I will then emphasize the effect of isolation on plant succession in remote islands as compared with less isolated areas. Finally, I will try to evaluate the modern threat of alien plant invasion and conclude with a future outlook on island vegetation.

The Island Biogeography Model and Vegetation Development

The island biogeography model of MacArthur and Wilson (1967) has captured the generally accepted fact that islands contain fewer species than their biotic source areas when compared on the same land-area basis. The isolation factor has been well demonstrated for mangrove species by Woodroffe (1987). Isolation as reflected in species impoverishment of forest canopy species has also been shown in the island vegetation treatment by Mueller-Dombois and Fosberg

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(1998). However, the equilibrium theory in the island biogeography model was an oversimplification. In this model, species equilibria were reduced to a simple function of rates of invasion and extinction in terms of island size and distance from biotic source areas. More factors have to be taken into consideration.

In addition to size or space, time in terms of succession and evolution is of equal importance as overriding the following factors here implied for vegetation development (V):

$$V = f(cl, g, d, fl, ac, e)$$

where: cl = climate, g = geoposition, d = disturbance, fl = flora, ac = access potential of a species, e = evolutionary/ecological properties of the species assembling in a vegetation cover.

The "d" factor, disturbance, is an integral part of vegetation development anywhere on the planet. It now includes human interference, which was not present in the formation of indigenous island vegetation. Likewise, the "cl" factor, climate, is universal for guiding vegetation development on islands as on continents. Geoposition with regard to such other "g" subfactors as geology, geomorphology, and ground (or soil substrate) also play the same role on islands and continents. Of course, the "g" subfactor geographic position is unique in vegetation development. For islands it includes the isolation factor, which is now broken by human interference.

The "flora" of an area is another universal factor in vegetation development. Note that it is only one factor among others, but it is a fundamental formation factor of any vegetation. The concept of flora differs from that of vegetation in that it relates to the plant species of broader areas and usually is treated in form of descriptions of plant species in books with pictures and keys for identification. In an island flora, only certain plants have access to a specific site or geoposition. The "ac" factor sets limits to the assemblage of species in a specific habitat or geoposition. The "e" factor determines which ecological/evolutionary adaptations of species are successful in a community. This, in turn, depends on the site potential or quality of a habitat, which is largely controlled by the climatic and geopositional factors as they vary over time.

THE ISOLATION EFFECT ON SUCCESSION

Not only did isolation have an effect on a simplified forest structure as reflected in the scarcity of canopy species in remote islands; it also had an effect on simplifying forest succession. This has become most evident through the phenomenon of canopy dieback observed and studied in Hawai'i, New Zealand, the Galápagos, Norfolk Island, and other areas (Mueller-Dombois and Fosberg 1998). Stand-level dieback of the leading canopy species usually releases the next generation of the same species to again resume dominance, as demonstrated for the montane *Metrosideros polymorpha* rain forest in Hawai'i (Boehmer 2005), the *Nothofagus solandri* var. *cliffordioides* forest in New Zealand (Wardle and Allen 1983), and the *Scalesia pedunculata* forest in the Galápagos Islands (Itow and Mueller-Dombois 1988). This type of secondary succession did function as a perpetuating monodominant growth cycle, known as "autosuccession" or "direct succession." Such simplified forest turnover may not continue in the presence of substantial invasion of alien species.

In the process of primary succession, involving geomorphic aging and volcanic shield breakdown, bogs and streams are formed in the rain forest environment of the younger Hawaiian Islands. In the bog-formation dieback, the main canopy species (*Metrosideros polymorpha*) re-grows only as a shrub or stunted tree. In older Hawaiian bogs, *M. polymorpha* seems to have evolved into dwarf races. There is no indigenous tall growing tree species adapted to paludification. The alien paperbark tree (*Melaleuca quinquenervia*), native to boggy habitats in New Caledonia and North Queensland, now assumes the forest replacement role in such paludified, formerly well-drained, rain forest habitats. This is an informative example of natural biodiversity limitation in a remote island, an enigma to former ecological research (Mueller-Dombois 2006).

Apparently, there has been little evolutionary development toward successional second-growth species through endemism in islands. Some dominant colonizer species have undergone evolutionary modification. The Norfolk Island pine (*Araucaria heterophylla*) is endemic in Norfolk Island, *Scalesia pedunculata* is endemic in the Galápagos Islands, and both *Metrosideros polymorpha* and *Acacia koa* are endemic in Hawai'i. But although many other endemic tree species evolved in these islands, endemic successional species evolved only rarely as replacers of the primary dominants in the major forest habitats.

The situation is different with regard to primary succession. Successional indigenous colonizer species certainly can be found, because primary succession is associated with changes in soil-substrate. In Hawai'i if one goes from the younger mountain Mauna Loa to the older mountain Mauna Kea in this subalpine zone, one will notice that *Metrosideros polymorpha* is replaced by *Acacia koa* and *Sophora chrysophylla*. *Acacia koa* is successional to *M. polymorpha* in mesic habitats in the course of primary succession, and *Sophora chrysophylla* has replaced *M. polymorpha* as a treeline species on Mauna Kea. This species change is associated with a substrate change from lava rock lithosol to deep volcanic ash regosol (Mueller-Dombois and Krajina 1968). Stemmermann and Ihsle (1993) analyzed dry-zone succession in a space-for-time study in the leeward lowland of Hawai'i and found that *Metrosideros polymorpha* dominates on the younger and *Dyospyros sandwicensis* on the older lava flows. Again, this is an example of primary succession involving endemic colonizer species.

SUCCESSION IN LESS-ISOLATED AREAS

In less-isolated forests, pioneer tree species are followed by successional species and these in turn by late-successional or climax species. For example, Curtis and McIntosh (1951) in Wisconsin arranged 22 canopy species by dominance according to their successional position by a "climax-adaptation number" from 1 to 10, with 10 being the most shade-tolerant climax species (*Acer saccharum*). This form of successional development has been called "obligatory succession" or "normal replacement succession" (Miles 1987).

Tropical rain forests on continents are known to have a multitude of canopy species. In a successional sense, such forests have two main groups of tree species. One group represents what is known as "primary forests" and the other as "secondary forests." Secondary forests typically form the replacement vegetation during early "secondary succession" after major disturbances. Primary forest may eventually redevelop during long periods without major disturbances.

Primary forests consist mostly of shade-tolerant long-lived tree species and secondary forests of shade-intolerant short-lived tree species. After MacArthur and Wilson (1967), the mathematical term "r" is used to characterize rapidly developing second-growth tree species and the term "K" for those forming primary forest or late-successional and climax tree species. There are other characteristics often associated with these two types of trees, such as large seeded, narrow-range dispersing, slow and tall growing with the "K" species and small seeded, widely dispersing, fast and not as tall growing with the second-growth or "r" species. The "r" and "K" distinctions are, of course, broad generalizations of species attributes, commonly referred to as species strategies. "Narrow-range dispersing" leads to isolation of stands within islands. This attribute can be applied to Southern Hemisphere gymnosperms (including species of *Agathis*, *Araucaria*, and some podocarps), which are climax forest species in New Zealand and other South Pacific islands. It may also apply to angiosperm trees that have lost their dispersal agents.

The vegetation ecologist Grime (1979) suggested that species behavior could be better generalized as displaying three strategies. He distinguished an "R" strategy for ruderal (weedy) species, a "C" strategy for highly competitive (aggressive) species, and an "S" strategy for stress-tolerant (very hardy) species. The problem with these species designations is that they are not fixed ecological properties. The assigned strategies are often modified by habitat constraints, competing

species, and other biotic interferences (e.g., disease factors). In the Hawaiian Islands, native forest-forming dominants can be considered "S" (stress-tolerant) keystone species. However, most native canopy trees are not shade-tolerant (that is, they cannot grow up under a closed tree canopy, such as do the late-successional [or climax] "K" species in less-isolated areas). Exceptions are some subcanopy shrubs and low-stature trees. In Hawai'i they include the tree ferns (*Cibotium* spp.) as robust keystone species. Thus, the native forest-forming dominants fall between the cracks of Grime's classification. There is as yet no category of stress-tolerant tree species that are intolerant of shade. Yet shade intolerance is not always a fixed attribute. It can become modified by site quality (e.g., enhanced tolerance with increased soil nitrogen).

Whistler (2002) listed six secondary successional canopy species as dominating mature forests in Samoa. Two of them (*Albizia chinensis* and *Falcataria moluccensis*) are alien species of more recent introduction. Another species (*Bischofia javanica*) may be an earlier introduction by Polynesian settlers, and the remaining three species (*Rhus taitensis*, *Alphitonia chinensis*, and *Elattostachys falcata*) are native. Thus, secondary forests in Samoa are only 50% native, and none of the second-growth species was identified as endemic to Samoa. The Samoan Islands form a rather coherent cluster in the South Pacific with Fiji and Tonga, where a greater assemblage of indigenous fast-growing secondary species can be expected. Thus, in the less-remote Pacific islands one can expect some secondary native forests forming impoverished analogs to the species-rich secondary forests of the continental tropics.

In New Zealand, *Metrosideros umbellata–Weinmannia racemosa* forests turn over into the same forest type, and *Nothofagus*-dominated forests remain *Nothofagus* forests, a process characterized by Stewart and Veblen (1983) as the "equilibrium model of vegetation change." This model assumes within-stand self-replacement of dominant species as the norm. Ogden (1988) gave examples of regeneration in pure and mixed stands of *Nothofagus* forests. For a mixed *N. solandri* var. *cliffordioides*, *N. fusca*, and *N. menziesii* stand he demonstrated that *N. fusca* is successional to the pioneer tree *N. solandri* var. *cliffordioides*, and the late-successional species *N. menziesii* is sequential to *N. fusca*. This is a "successional enrichment sequence" of three congeneric endemic tree species rather than a complete "successional replacement sequence" of unrelated taxa. In the rain forest environment of Hawai'i, Stemmermann (1983) detected a conspecific succession. There the leaf-pubescent pioneer variety *Metrosideros polymorpha* var. *polymorpha* is being replaced by the leaf-glabrous variety *M. polymorpha* var. *glaberrima*. These examples show that in remote islands evolutionary tendencies exist that work in the direction of diversification of successional tree species. This trend of successional replacement by different taxa now seems to be radically accelerated by the invasion of alien species.

THE MODERN THREAT OF ALIEN PLANT INVASION

The prevailing view in Hawai'i today is that alien plants will overgrow and outcompete all native vegetation. Total replacement of native vegetation is certainly true for most lowland sites on the older high islands. This is no surprise in view of the great disturbance history and the active promotion of alien plant propagation, a land-management practice considered necessary up to the 1980s (Cuddihy and Stone 1990). For example, aerial seeding of the alien *Leucaena leucocephala* was practiced in the 1920s to stem accelerated soil erosion after overgrazing and frequent human-set fires had destroyed most existing natural vegetation. Today *L. leucocephala* scrub is a widespread alien vegetation cover in the leeward lowlands of all Hawaiian high islands. Some old stands died between 1986 and 1991. After a thorough study, Ikagawa (1993) concluded that the *Leucaena* dieback was triggered by an introduced psyllid (*Heteropsylla cubana*) in cohort stands that appeared predisposed to die from old age and other stresses. On leeward ridges in the Honolulu area two indigenous shrubs, *Sida fallax* and

Dodonaea viscosa, persisted in some dieback stands. Likewise, *Leucaena* persisted as a dominant shrub-tree by autosuccession. It thus can now be considered a climax species in the leeward hills. In some disturbed rain forests on O'ahu, *Leucaena leucocephala* occurs as a spontaneous invader, but it disappears when overgrown by taller trees, thus having only a pioneer role as a "second-growth" species. Many other second-growth species have been introduced to Hawai'i. They now often appear as spontaneous invaders on former sugarcane land. From there they can easily advance into disturbed native rain forests.

An example is the large (>100 ha) cutover rain forest next to the 1977 lava flow in the Kalapana area on Hawai'i Island. There a native lowland rain forest was logged in 1983–1984 to make wood chips for electricity generation (Mueller-Dombois 1985). The general prediction was that such a clear-cut area would recover as a weed patch. A subsequent study of the early recovering vegetation by Grossman (1992) revealed the appearance of many small seedlings of *Metrosideros polymorpha*. A revisit after 20 yr showed a surprising recovery of trees of this native dominant. Alien trees of "second-growth" species, such as *Trema orientalis*, *Melochia umbellata*, *Psidium cattleianum*, and some *Falcataria moluccana*, now grow together with *Metrosideros polymorpha*. *Metrosideros polymorpha* individuals are currently 7–12 m tall. They have grown much faster in height than on the adjacent 1977 'a'ā lava flow. On this logged area with fertile soil, *M. polymorpha* has shown its adaptive capacity. Here it grows as fast as the alien "second-growth" trees. An exception among the other second-growth species is the nitrogen-fixing tree *Falcataria moluccana*. By growing very fast and tall, it can overgrow the otherwise dominant *M. polymorpha*. Wherever this overgrowth occurs in this lowland rain forest environment, *M. polymorpha* dies from lack of light under the canopy of the *Falcataria* trees. This alien species should be an obvious target for control through silvicultural management. Girdling *Falcataria* in the sapling stage would seem a cost-efficient measure. *Psidium cattleianum* is another troublesome alien invader. It is promoted in sites scarified by feral pigs. In such sites, *P. cattleianum* forms dense thickets. It can also spread clonally, and this gives it an advantage over nonclonal trees. Where pigs are absent it will distribute itself more sparsely among other trees. In the absence of feral pigs it will not necessarily outcompete *Metrosideros polymorpha*.

A FUTURE OUTLOOK ON ISLAND VEGETATION

The problem of alien plant invasion is not as simple as the common "threat assumption" in Hawai'i that all native vegetation will eventually be overgrown by alien species. In fact, the situation is very complex but not hopeless. Native vegetation can be maintained as well as restored by appropriate silvicultural management. There is no doubt that the influx of alien plants has resulted in a new natural dynamic, which has taken its own course. The result will be an increasing biodiversity from species packing. Monodominant canopy tree patterns will most likely decline and tree diversity patterns will increase in unmanaged natural landscapes. Species extinction will not be a necessary consequence of species packing.

We know little as yet about species extinction by competition among native and alien plant species. Species extinction, however, has become very obvious through habitat loss. Awareness with well-thought-out cost-efficient conservation strategies is a necessary pathway to prevent undue habitat and species loss. A step in this direction is the Pacific-Asia Biodiversity Transect network (PABITRA), a program of the Biodiversity Task Force of the Pacific Science Association. The objective of PABITRA (www.botany.hawaii.edu/pabitra) is mutual capacity building for ecosystem research and conservation on a community basis with Pacific islanders. Biodiversity is one of the most important renewable resources within the human support system of the Pacific islands. Climate change promotes an additional level of dynamic plant behavior, such as the preferential expansion of vines in the enhanced carbon dioxide atmosphere. Great efforts are needed in re-

search and natural area management to understand and properly manage the new vegetation dynamic as it evolves under global change.

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